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Microvertebrates from the Rhaetian bone beds at Blue Anchor Bay, Somerset

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Abstract

The cliff and foreshore sections at Blue Anchor Bay, north Somerset, provide a detailed picture of the transitional Triassic–Jurassic succession. The site has been recorded as a location for fossil fishes for over 200 years, and yet the assemblages from the bone beds have not been described. Here, we present new observations on the two bone beds and find major faunal differences: the classic basal bone bed at Blue Anchor Bay contains an assemblage dominated by osteichthyan teeth, unexpected because elsewhere the ichthyofauna is usually dominated by chondrichthyans. The upper bone bed at Blue Anchor Bay is indeed more typical, being dominated by teeth of hybodont chondrichthyans. We report two unusual finds, first five teeth of the rare shark *Parasycylloides turnerae*, only the fifth such record in the UK. Further, we report here for the first time a tooth of the pycnodontiform *Eomesodon*, the first report of this taxon from the Triassic of the UK or Europe. The two bone beds are distinguished not only by different assemblages, but also by evidence of different degrees of anoxia and water depth: the upper bone bed contains abundant pyrite and marcasite, indicating highly anoxic conditions, and perhaps deposition in deeper water than the basal bone bed.

1. Introduction

The Rhaetian (205.7 ± 0.4–201.4 ± 0.2 Ma; Gradstein *et al*. 2020) is the final stage of the Triassic, during which a continental-scale marine transgression occurred over much of Europe (Cross *et al*. 2018; Lovegrove *et al*. 2021). This caused dramatic changes in the resulting deposits, since the depositional environments evolved from terrestrial to shallow marine environments (Cross *et al*. 2018; Lovegrove *et al*. 2021). In the UK, the long-term continental red-bed deposits of the Mercia Mudstone Group transitioned upward into the partially marine deposits of the Blue Anchor Formation, and then the fully marine units of the succeeding Penarth Group (Lovegrove *et al*. 2021). Faunas from the Rhaetian are dominated by marine taxa that occupied the epicontinental seas, with terrestrial reptiles and synapsids limited to the various islands remaining above sea level (Whiteside *et al*. 2016; Lovegrove *et al*. 2021).

These marine Rhaetian faunas (Duffin 1999; Storrs 1999) include chondrichthyan fishes (hybodonts and neoselachians), Osteichthyan fishes (actinopterygians, including teleosts, and sarcopterygians, such as lungfishes and coelacanths) and marine reptiles (ichthyosaurs, plesiosaurs, placodonts and thalattosaurs). These faunas are mainly preserved in bone beds, and these are common throughout the British marine Rhaetian (Suan *et al*. 2012). These Upper Triassic deposits are mainly found in localities in the SW of England, around Bristol (Agassiz 1835; Foffa *et al*. 2014; Allard *et al*. 2015; Cross *et al*. 2018), in the Mendips (Nordén *et al*. 2015; Moreau *et al*. 2021; Ronan *et al*. 2020), in north Somerset (Richardson 1911; Tayler *et al*. 2023), Devon (Korneisel *et al*. 2015) and south Wales (Suan *et al*. 2012; Williams *et al*. 2022).

In Somerset, these marine Rhaetian deposits are particularly well exposed along the north coast, on the shore near Watchet, in a section from Blue Anchor Point to Lilstock (Sykes 1977; Warrington & Whittaker 1984). Blue Anchor Point is thus at the western extremity of the exposure of these marine deposits (Figure 1). This is also the type locality of the Blue Anchor Formation, corresponding to the uppermost part of the Mercia Mudstone Group (Warrington *et al*. 1980; Warrington & Whittaker 1984).

Here, we describe the microvertebrate remains found in the two bone beds at Blue Anchor Bay, the Basal Bone-Bed and an upper bone bed mentioned by Richardson (1911). These are significant as the succession here marks the type section of the Blue Anchor Formation, and was part of the supporting geological sections used to make the case that the St Audrie's Bay section nearby should be the Global Stratigraphic Section and Point (GSSP) for the Triassic–Jurassic boundary (Warrington *et al*. 1994).
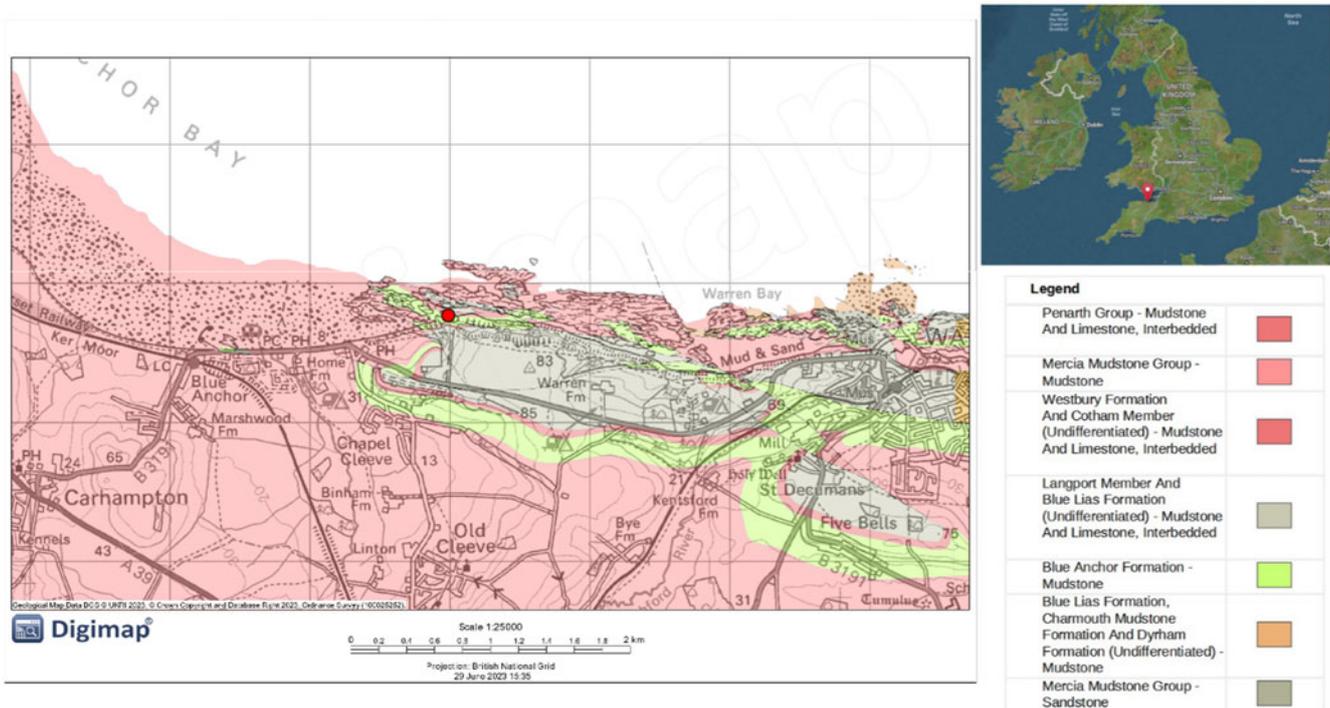
Figure 1. (Colour online) Geological map of Blue Anchor Bay. The red dot indicates the location of the bone beds sampled. © Crown Copyright and Database Right 2023 Ordnance Survey (Digimap Licence).

2. Geological setting

The Penarth Group is well exposed on the foreshore at low tide and in the cliffs at Blue Anchor Point (ST 04048 43773), north Somerset (Figures 1 and 2). The succession spans the upper part of the Mercia Mudstone Group and most of the Penarth Group, terminating in the lower part of the Hettangian, thus encompassing the Triassic–Jurassic boundary (Richardson 1911). All these Mesozoic deposits are disrupted by a series of normal faults, forming part of the classic view (Figure 2A) of Blue Anchor Point. Among these faults, the westernmost is the main fault (Glen *et al.* 2005, figure 9c), and west of this main fault, the cliff comprises the red beds of the Mercia Mudstone Group. The Blue Anchor Formation and Penarth Group beds to the east of the main fault are slightly folded (Richardson 1911), with the anticlinal axis pointing towards the foreshore, confirming that the deposits of the cliff and the foreshore were once contiguous, forming a single deposit (Figure 2A).

The first geological account of the Blue Anchor location was by Horner (1816, pp. 366–372), who reported high cliffs up to 100 feet (30 m) high on the coast between Minehead and the River Parrett, and reported alternations of the red siltstones (Mercia Mudstone Formation) and the 'lyas' (Rhaetian plus Early Jurassic), but he divined correctly that this appearance had been generated by faults ('dislocations', as he calls them). He walked from the River Parrett in the east, and encountered the Lias on the shore at Lilstock, and walked past Watchet to Blue Anchor Bay, which marks the western extent of these units. He noted the way in which the bedding of the Rhaetian and Lias shows up as great sweeping ridges of rock across the rocky shore, and he reported ammonites and other typical Lower Jurassic fossils. He reports black shales, some with bituminous contents, but it is not clear that he encountered the Rhaetian bone bed.

Eight years later, a more professional study was published by Buckland and Conybeare (1824). There they presented a map and categorized the stratigraphy. They reported the Triassic and Jurassic of the north Somerset coastline (Buckland & Conybeare 1824, pp. 298–301), and identified black-coloured shales beneath the regular Lias, presumably what we call now the Westbury Formation. They matched these black shales, and especially their bone beds to similar occurrences they had seen at Aust and Westbury Garden Cliff (see also Cross *et al.* 2018; Williams *et al.* 2022). In a lengthy footnote, they note that the bone bed had been identified first by Robert Anstice 'near Watchet', (see Duffin 2009, p. 107) but they do not specify exactly where, whether to the east (Doniford, Lilstock) or west (Blue Anchor Bay) of the town, but more probably to the east, and we describe further historical detail in our account of Doniford Bay (Tayler *et al.* 2023).

The locality was then studied by De la Beche (1839, pp. 196, 232) who reported the Mercia Mudstones and Lias along the coast and inland, from St Decumans past Watchet to Blue Anchor Bay. He noted the gypsum in the red beds portions of the Mercia Mudstones Group, and the overlying 'variegated marls' (Blue Anchor Formation), and the Lias above that, but did not refer to the black shales (Westbury Beds) or the bonebed at the base.

Some 20 years later, the Rhaetian was widely recognized as a distinct temporal unit but termed the 'Zone of *Avicula contorta*' by Wright (1860) in his detailed review of many of the classic sections around Bristol and south Wales. This succession included all the mudstones and marls between the red Keuper marls (Mercia Mudstone Group) and the White Lias, and Wright did assign these to the uppermost Triassic. Wright (1860, p. 336) drew attention to the bone bed at Watchet but did not comment on Blue Anchor Bay in particular. Boyd Dawkins (1864) extended that work with evidence from his visits to the sections around Watchet, including to the west of that town, even though he did not refer to Blue

Figure 2. (Colour online) Field photographs at Blue Anchor Point. (A) Overview of the cliffs showing the faults. (B) Field photograph of a fallen rock showing pink gypsum veins. (C) Field photograph of the basal bone bed on the foreshore. (D) Field photograph of the upper bone bed and *Pleurophorus* bed on the foreshore. Abbreviations: BBB: basal bone bed; PB: *Pleurophorus* bed; RC: rip-up clast; SB: Sully bed; UBB: upper bone bed. Limits of beds are indicated by the black segments.

Anchor Bay. He equated the 'Zone of *Avicula contorta*' with the Rhaetic of Germany, and reported his fossil finds. In particular, he reported a bone bed in the Williton Member (Sully Beds), below the base of the Westbury Formation, and a fossil he found ten feet under this basal bone bed, comprising common Rhaetian fish taxa and a mammal tooth on which he based the mammal species *Hypsiprymnopsis rhaeticus*. However, the tooth has been lost, and it remains a tantalizingly early mammal record that has not been replicated since either here or elsewhere.

The first detailed stratigraphic description at Blue Anchor Bay was by Richardson (1911), who identified on the shore four bone beds from the Westbury Formation and named three of them (Figure 3A). He also reported the vertebrate remains from the Blue Anchor Formation mentioned by Boyd Dawkins. Despite the description of these bone beds, only sporadic studies of the assemblages have been made since then. Thus, Sykes (1974) found two teeth of the shark *Pseudodalatias barnstonensis* (Sykes 1971) at Blue Anchor Point. Hamilton and Whittaker (1977) also reported common Rhaetian fish assemblages, together with plesiosaur vertebrae. Further, a number of sarcopterygian remains have been found on the shore, including the gular plate of an indeterminate coelacanth in a bone bed from the Westbury Formation (Hauser & Martill 2013), and a partially articulated skeleton of the dipnoan ? *Ceratodus* sp. also from the Westbury Formation (Duffin 1999). An important reptile discovery from the basal Westbury Formation bone bed is the thalattosaur *Pachystropheus rhaeticus* based on vertebrae and limb bones from here and from Westbury Garden Cliff in Gloucestershire (E. von Huene 1935; Storrs 1993; Storrs & Gower 1993; Storrs *et al.* 1996).

Since the cliff is difficult to access (Richardson 1911) and the Rhaetian horizons are often covered by banked beach shingle, the Penarth Group of Blue Anchor Point has mainly been studied from exposures on the foreshore. Nonetheless, the cliff is the location of the type section of the Blue Anchor Formation, the uppermost part of the Mercia Mudstone Group (Warrington *et al.* 1980;

Warrington & Whittaker 1984). On the shore, the uppermost part of the Blue Anchor Formation and the basal part of the Penarth Group, the Westbury Formation, are represented by a series of limestone beds separated by black shales beds of various thickness. Richardson (1911, pp. 15–20) made the first detailed stratigraphic log (Figure 3A), reproduced by Edwards (1999, figure 26, 27). Our stratigraphic log (Figure 3B) was made by C. Duffin in his unpublished PhD thesis in 1980, supplemented with our field observations in 2023.

The differences between the two logs (Figure 3A, B) can be explained by the fact that the beds are not continuous, and that the logs were made in slightly different locations, also including Richardson's (1911) observations from the cliff, and with 69 years of erosion separating the two observations. This erosion is important at Blue Anchor Point, since storms regularly occur, pulling off parts of the cliff. This was reported by Edwards (1999), who specified that rocks fell from the cliff in a storm in 1996 after he took the photographs he presented. Such fallen rocks, of various sizes, sometimes more than 1 m across, cover some parts of the shore under the cliffs, and some of them contain vertebrate remains in bone beds (Figure 2B). These remains can measure dozens of centimetres, but the fact that their stratigraphic origin is uncertain lowers their scientific interest.

Among the beds found on the foreshore, two bone beds with millimetre-size vertebrate remains can easily be found low in the Westbury Formation, although Richardson (1911) mentioned four such bone beds. We identify his basal Westbury Formation bone bed, and a second bone bed 5 m higher, but could not identify the other two bone beds, including that named 'The Clough' (Richardson 1911, bed 27), which Sykes (1977) also failed to find.

The lower bone bed is the Basal Bone-Bed (bed 33 in Richardson 1911) at the base of the Westbury Formation. It lies on the upper surface of the Blue Anchor Formation, which is eroded and bioturbated by *Thalassinoides* burrows (Figure 2C). These burrows are filled with deposits of the Basal Bone-Bed, as
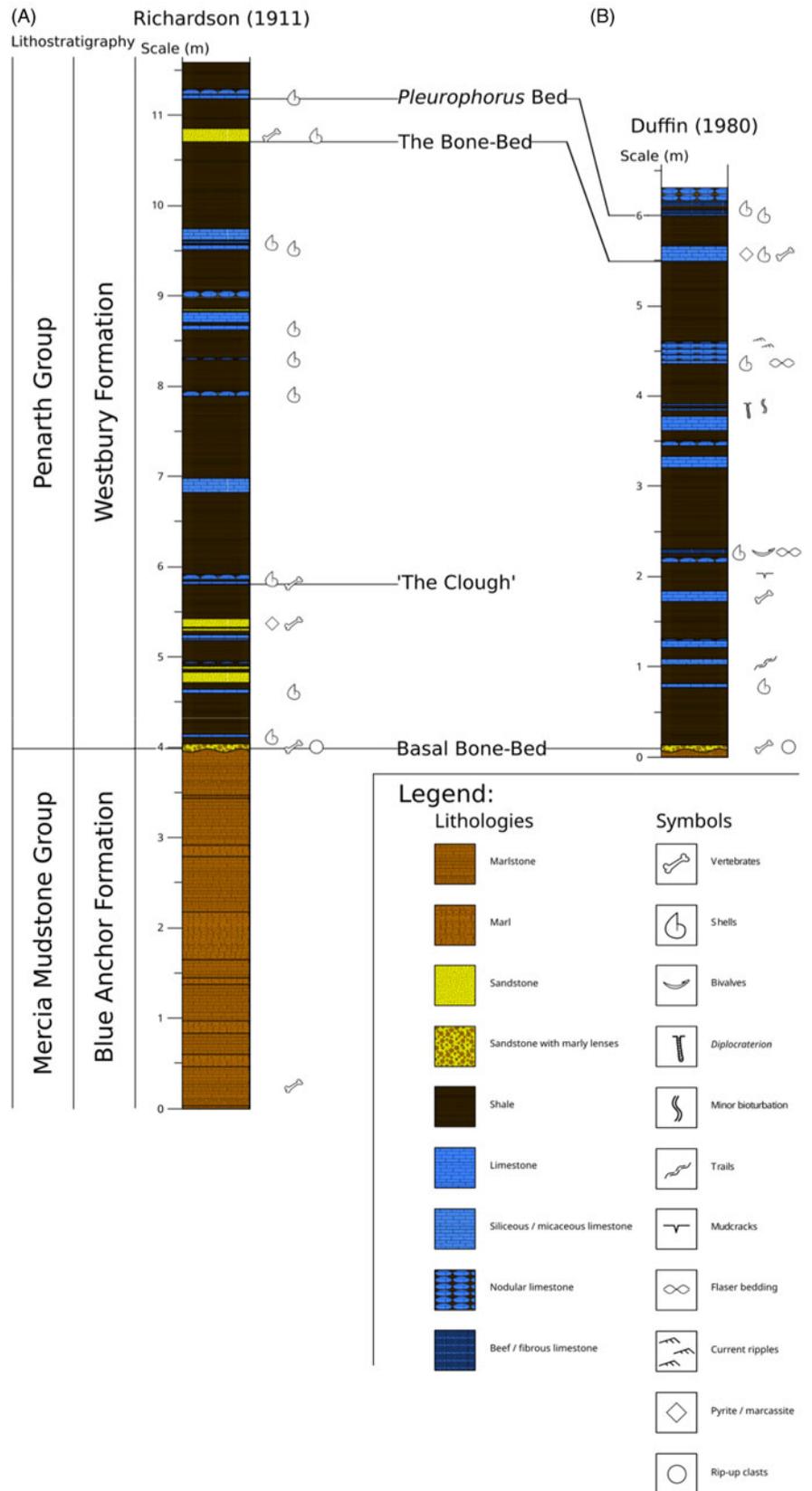
Figure 3. (Colour online) Stratigraphic logs of the section on the foreshore at Blue Anchor Point. (A) Section described by Richardson (1911). (B) Section described by *C. Duffin* in his unpublished PhD thesis in 1980.

depicted by Korneisel *et al.* (2015, figure 8) from Charton Bay, Devon. The bone bed also contains rip-up cream-coloured pebbles from the Sully Bed, the uppermost unit of the Blue Anchor Formation, suggesting deposition during storm events (Figure 2C).

The upper bone bed is Richardson's (1911) bed 15, 'The Bone-Bed', situated just under the *Pleurophorus* bed (bed 13 in Richardson 1911), whose *Pleurophorus* shell remains make it easy to recognize. This upper bone bed (Figure 2D) comprises layers of

hard, grey, calcareous sandstones (Richardson 1911) that are finer grained and more clay-rich at the base and coarsen upwards. Quartz grains from the base show solution pits whereas those from higher parts of the bone bed show euhedral quartz overgrowths that formed after deposition in the more porous conditions there (Antia & Sykes 1979). Apart from the microfossils, we identified marcasite crystals in the bone bed, indicating euxinic deposition conditions.

The underlying Blue Anchor Formation at and east of Blue Anchor Bay was described in detail by Mayall (1981). In particular, he wrote about the Sully Beds of north Somerset and Penarth in South Wales, renamed by him the Williton Member, a unit varying in thickness from 0 to 3 m. Although it is named after the village Williton, near St Audries Bay, Mayall (1981, pl. 1) illustrated some key features from Blue Anchor Bay, including the base of the unit, marked by *Diplocraterion* burrows, as well as trace fossils throughout, bivalves, and some horizons with mud cracks. All evidence shows that, as long suspected, the Williton Member was deposited in a fully marine environment.

More recently, when St Audrie's Bay was a candidate GSSP for the Triassic–Jurassic boundary, highly detailed studies of the stratigraphy of the Penarth and Lias groups along the whole north Somerset section, including Blue Anchor Bay, were completed, providing a thorough basis for comparison of the succession to the international standard stratigraphic scale, according to biostratigraphy (dinoflagellates, ammonites), stable isotopes and magneto-stratigraphy (e.g. Hesselbo *et al.* 2004; Hounslow *et al.* 2004; Korte *et al.* 2009; Bonis *et al.* 2010).

3. Materials and methods

The microfossils studied here come from both bone beds. We studied three rock samples, two from the basal Westbury Formation bone bed, and one from the upper bone bed, the first collected in 2019 and the other two in 2023. In the lower bone bed, millimetre-sized fish remains can be seen with the naked eye in the sediment, which comprises greyish gritty calcareous sandstones with cream-coloured mudstone lenses. The upper bone bed sample is also a calcareous sandstone but appears more massive and with more concentrated microvertebrate remains.

The samples were processed according to standard methods as in other studies (e.g. Cross *et al.* 2018). They were put in a 2 L acid bath made of acetic acid (5% volume concentration in water) with sodium carbonate (7.5 g.L−1) and tri-calcium di-orthophosphate (2 g.L−1) acting as a buffer to protect the fossils from acid digestion. After immersion for 48 hours, the resulting fragments were washed with water through a series of sieves with meshes of 2 mm, 500 µm and 180 µm to separate them from the finer clay fraction which is washed away. The 500 µm and 180 µm fragments where then gathered and dried separately and the 2 mm portion was processed a second time following the same protocol, and this was repeated until all the matrix of the rock samples was fragmented into pieces smaller than 2 mm.

The microfossils were then picked from the 500 µm and 180 µm samples under a Nikon SMZ445 C-LEDS stereomicroscope. When possible, fossil specimens were identified and sorted by species and type (tooth, scale, bone), and the best-preserved specimens were photographed. Identified specimens were also counted in the same way as in other studies (e.g. Cross *et al.* 2018). Thus, *Rhomphaiodon minor* teeth were counted when there was at least the central cusp with a part of the root. For *Lissodus minimus* teeth, they were counted when the central cusp was present with the

labial node. All *Parascylloides turnerae* teeth were counted, given the fact they all had an intact central cusp. *Synechodus rhaeticus* and *Pseudodalatias barnstonensis* teeth were too fragmentary to be counted. For osteichthyan teeth, *Gyrolepis albertii*, *Birgeria acuminata* and *Saurichthys longidens* teeth were counted when the apical cap was present with at least a portion of the shaft. For *Lepidotes* sp. and *Sargodon tomicus*, teeth were counted when they had their cap unbroken with shaft. For other remains, all identified specimens were counted. All specimen photographs were taken with a Leica M205C microscope using multifocus photography methods provided by the Leica Application Suite v4.12. These images were then processed with GIMP v2.10.34 software to remove the background and adjust the colour balance.

4. Systematic palaeontology

4.a. Chondrichthyes

4.a.1. Lissodus minimus (Agassiz, 1839)
A total of 86 specimens were found (Figure 4A–D), 66 from the upper bone bed and 20 from the basal bone bed. Only crowns of teeth have been found, most of them incomplete. These narrow crowns consist of a small flattened central cusp, sometimes flanked by a pair of lateral cusplets. The crown is ornamented with ridges that are generally perpendicular to the cutting edge, running from this edge to the base of the crown. A labial node is also present at the base of the central cusp.

There are variable tooth types present in the heterodont dentition, and we have identified complete anterior, anterolateral and lateral teeth, but only incomplete posterolateral and posterior teeth. The most common teeth are anterolateral teeth, often lacking both lateral extremities.

4.a.2. Rhomphaiodon minor (Agassiz, 1837)
This species (Figure 4E–I) has been found in both the upper (41 teeth) and basal bone beds (12 teeth). Complete teeth are symmetrical, and their crowns consist of a row of an odd number of cusps, with the cusps being taller towards the centre. The central cusp is generally significantly larger than the lateral cusplets. The cusps are conical, slightly flattened labio-lingually, and their apices are generally slightly curved lingually. The cusps are also ornamented on both faces with strong, widely spaced ridges from the base of the cusps almost to the tip. The crown is supported by a root that expands lingually and presents a number of foramina on both lingual and labial faces.

Four more teeth (with one from the basal bone bed) could also belong to *R. minor* or perhaps to '*Hybodus*' *cloacinus* Quenstedt, 1858. There is a debate about this last species, sometimes referred to as *Polyacrodus cloacinus*, the generic allocation remaining uncertain (Skinner *et al.* 2020).

4.a.3. Parascylloides turnerae Thies et al., 2014
Five teeth of this species have been found (Figure 4J, K), with only one from the basal bone bed. The teeth consist of an elongate, massive and symmetrical central cusp, flanked by two small lateral cusplets whose bases are fused with the main cusp base. The central cusp is curved lingually, and both its labial and lingual faces have widely spaced ridges originating at the base and extending almost up to the tip. The root of the tooth extends lingually, giving it a laterally flattened ovoid shape in basal view. A few foramina are present on the labial and lingual faces of the root.
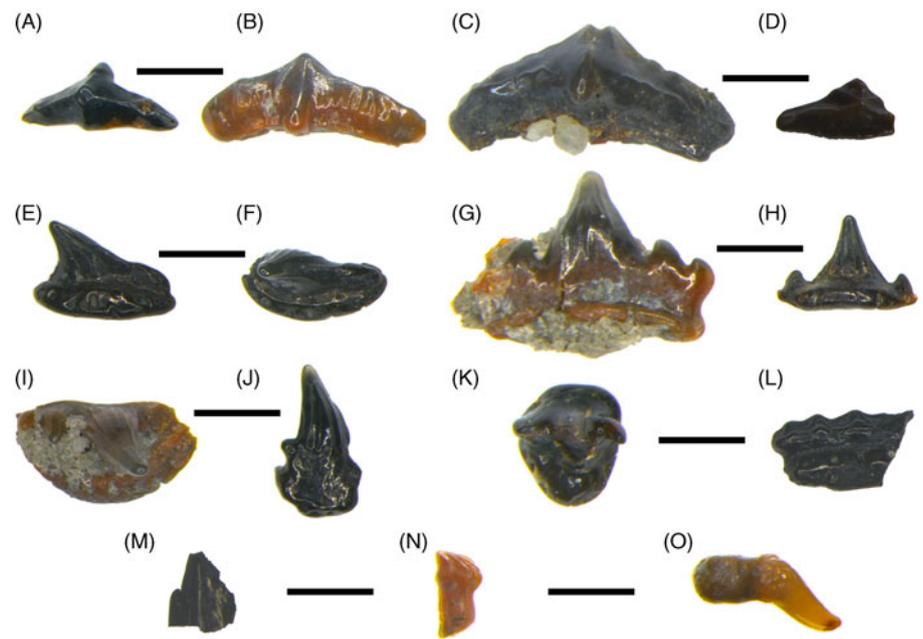
Figure 4. (Colour online) Chondrichthyan teeth from the upper and basal bone beds at Blue Anchor Point. (A, B) *Lissodus minimus* anterolateral teeth: (A) BRSUG 29974-26 in occlusal view; (B) BRSUG 29974-23 in labial view. (C) *Lissodus minimus* anterior tooth BRSUG 29974-25 in labial view. (D) *Lissodus minimus* lateral tooth BRSUG 29974-66 in occlusal view. (E–I) *Rhomphaiodon minor* teeth: (E, F) BRSUG 29974-28 in lingual (E), and occlusal (F) views; (G) BRSUG 29974-31 in labial view; (H) BRSUG 29974-27 in lingual view; (I) BRSUG 29974-29 in occlusal view. (J, K) *Parascylloides turnerae* teeth: (J) BRSUG 29974-39 in labial view; (K) BRSUG 29974-40 in occlusal view. (L) *Synechodus rhaeticus* tooth BRSUG 29974-32 in labial view. (M) *Pseudodalatias barnstonensis* lower tooth fragment BRSUG 29974-43 in labial or lingual view. (N, O) ?*Pseudocetorhinus pickfordi* lateral teeth: (N) BRSUG 29974-182 in lateral view; (O) BRSUG 29974-190 in lateral view. Scale bar: 1 mm, except for K, N and O: 500 μm.

The species was first described from teeth from a railway cutting near Barnstone, Nottinghamshire (England) and three localities in the Federal State of Lower Saxony (Germany), all of Rhaetian age (Thies *et al.* 2014). The species has since been recorded in two other localities of the Rhaetian of England, at Aust Cliff, Gloucestershire (Cross *et al.* 2018) and Saltford, Somerset (Moreau *et al.* 2021). Whiteside and Duffin (2021) also mentioned its occurrence at a new locality near the 'Microlestes' Quarry of Holwell, Somerset. Our discovery of *Parascylloides turnerae* in the basal bone bed at Blue Anchor Point is thus the fifth confirmed occurrence of the taxon in the UK.

4.a.4. *Synechodus rhaeticus* (Duffin, 1982)
Only one tooth of this species has been found in the upper bone bed (Figure 4L). It consists of the lateral portion of a tooth, presenting a crown with three thick, pointed and flattened cusplets in a row, supported by a root of similar size. The cusplets are ornamented by a few thick ridges that extend from the apex to the middle of the crown, where a row of labial nodes is located, each node being located beneath a cusplet.

4.a.5. *Pseudodalatias barnstonensis* Sykes, 1971
Only a portion of a lower tooth of this species has been found, from the upper bone bed (Figure 4M). This specimen corresponds to the upper part of the crown. Complete teeth of this species have a triangular shape, with a thin serrated cutting edge, but only one side of the cutting edge with one serration is present in our specimen.

4.a.6. ?*Pseudocetorhinus pickfordi* Duffin, 1998a
Four sharks' teeth with an atypical shape have been found in the basal bone bed. Three of them (Figure 4N) have a crown resembling morph 2 placoid scales (see below), with a sloping labial face with a drop-like shape ornamented with at least three bulging ridges running from the lower part of this face to its apex. Beneath this crown an elongate, cylindrical root is present, with no ornamentation. In a further specimen (Figure 4O), the root is similar, but the crown is pointed and much more elongated,

bending lingually. Some ridges are also present, but they are less bulging and do not extend towards the apex, being confined to the labial base of the crown. Most of the crown is thus unornamented.

Because this last specimen has an elongate, pointed and unornamented crown, and resembles the three other specimens, but with a more developed crown, the four specimens are attributed with some trepidation to *Pseudocetorhinus pickfordi*. The four specimens would likely be lateral teeth.

4.a.7. Other chondrichthyan remains
Two neoselachian vertebrae have been found in the upper bone bed (Figure 5A, B). They have a cylindrical shape with a concave lateral face and are only slightly eroded.

4.a.8. Denticles
Seventy-two denticles have been found. Among them, three denticles from the basal bone bed possessing a thick, tall and rounded base and a flat and circular crown (Figure 5C) have not been assigned to a specific denticle type. The other denticles are sorted based on the classification proposed by Reif (1978), and each type is further described in the following subsections.

4.a.8.a. Placoid scales.
A total of 66 placoid scales have been found, with only three from the upper bone bed. Two of them are fragmentary, one being a denticle base and the other an incomplete crown. This incompleteness made them impossible to classify more precisely. Among the other specimens, that comprise most of the crown when they are not complete, four morphotypes have been found.

- Morphotype 1 (Figure 5D, E) is the most abundant type with 48 specimens, three from the upper bone bed. They correspond to morphotype 1 in Cross *et al.* (2018). They have a rounded base with a central depression, and a posteriorly curved paddle-like crown, with at least three thick vertical ridges on the anterior face that stand out on the edge of the crown.
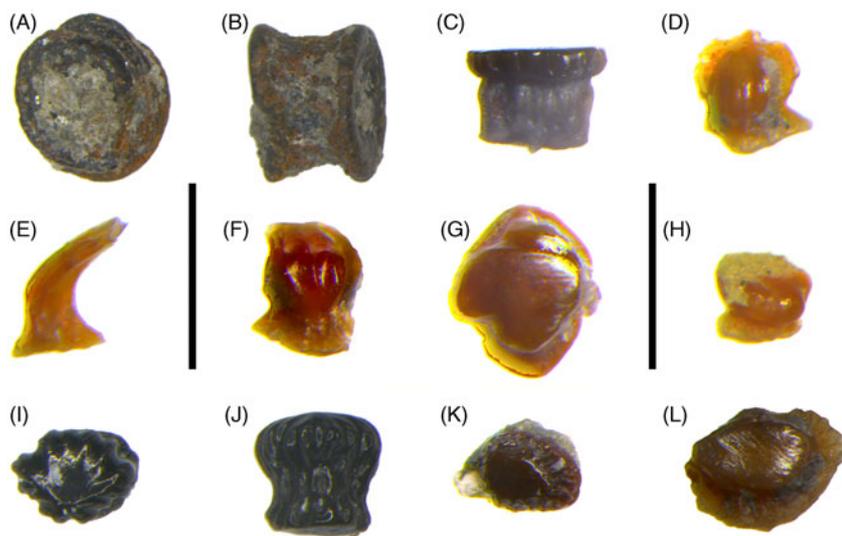
Figure 5. (Colour online) Chondrichthyan denticles and vertebrae. (A, B) Neoselachian vertebra BRSUG 29974-10 in anterior or posterior (A) and lateral (B) views. (C) Miscellaneous denticle BRSUG 29974-77 in lateral view. (D, E) Morphotype 1 placoid denticles: (D) BRSUG 29974-178 in anterior view; (E) BRSUG 29974-76 in lateral view. (F) Morphotype 2 placoid denticle BRSUG 29974-180 in anterior view. (G) Morphotype 3 placoid denticle BRSUG 29974-183 in exterior view. (H) Morphotype 4 placoid denticle BRSUG 29974-185 in anterolateral view. (I–L) Hybodontid denticles: (I, J) BRSUG 29974-9 in exterior (I) and anterior or posterior (J) views; (K) BRSUG 29974-81 in exterior view; (L) BRSUG 29974-79 in exterior view. Scale bar: 1 mm, except A and B: 2 mm, and D-H: 500 μm.

- Morphotype 2 (Figure 5F) is less well represented, with only five specimens from the basal bone bed. They correspond to morphotype 2 in Cross *et al.* (2018). They are similar to morphotype 1, but with a thick rounded neck and crown, and usually more ridges on the anterior face.
- One specimen of morphotype 3 placoid scales (Figure 5G) has been found in the basal bone bed. It has a high neck, and a small top with three eroded thick ridges. The occlusal view resembles that illustrated in Landon *et al.* (2017, figure 5E).
- Eight morphotype 4 placoid scales (Figure 5H) have been found, confined to the basal bone bed. These denticles have a flattened crown that is bent anteriorly, and with vertical ridges on the anterior part of the crown edge. Morphotype 4 denticles resemble morphotype 2 denticles but they have a flatter and lower crown on which ridges are less visible.

4.a.8.2. Hybodontid scales. Three hybodontid scales have been found. The first (Figure 5I, J), from the upper bone bed, has a bulbous crown, supported by a thick neck, and is posteriorly flattened. Thick ridges arise from the base of the root to the top of the crown are also present all around the denticle. The last two specimens (Figure 5K, L) are from the lower bone bed, and they have a large, ovoid base and a quite flat but eroded ovoid top. These two denticles are eroded, making their classification uncertain.

4.b. Osteichthyes

4.b.1. Gyrolepis albertii Agassiz, 1835
There are 66 *Gyrolepis* teeth (Figure 6A), mainly from the basal bone bed (only two are from the upper bone bed). The teeth are elongate, conical, with a slight sinusoidal curvature towards the apex, which is covered with an unornamented, translucent, conical and sharp acrodin cap. The shaft is smooth, with fine wrinkles, and the base is slightly flared. However, around half of these teeth are incomplete, lacking either the base or the cap.

4.b.2. Birgeria acuminata (Agassiz, 1835)
There are 20 teeth (Figure 6B) from both the upper (four) and basal bone beds (16). The teeth generally lack the basal part of the shaft. These teeth are conical, elongate, rarely slightly curved towards the apex, and covered on the top with a translucent, conical and sharp acrodin cap. This cap possesses straight ridges going from its base

to the tip. The shaft is finely ridged from the base to the boundary with the cap, which is generally very clearly defined.

In previous studies, this taxon was often combined with *Saurichthys longidens* into the taxon *Severnichthys acuminatus*, following Storrs (1994) who synonymized the two taxa based on isolated teeth and jaw fragments. *B. acuminata* and *S. longidens* teeth were then considered morphotypes of *S. acuminatus*. Diependaal and Reumer (2021) argued that this taxon is a *nomen dubium*, based on morphological differences between *B. acuminata* and *S. longidens* in terms of their taxonomic allocation to two distinct families, and their overall body shapes, as Tintori and Lombardo (2017) had already stated, and we treat them as distinct taxa here.

4.b.3. Saurichthys longidens Agassiz, 1835
This taxon (Figure 6C) is present in both the upper bone bed (four teeth) and the basal bone bed (five teeth). One specimen from the basal bone bed is a small tooth attached to a jaw fragment. The apical cap of these teeth is conical, translucent and unornamented, and the shaft has thick vertical ridges going from the base to the cap. For the complete tooth, the shaft is smoother, and the apex is slightly curved. One large, conical tooth with thick ridges on both shaft and cap has also been found and could be an abnormal *S. longidens* tooth.

4.b.4. Sargodon tomicus Plieninger, 1847
This species has two types of teeth: incisiforms (Figure 6D) and molariforms (Figure 6E), both of which have been found at Blue Anchor Point. Molariform teeth occur in both bone beds (two from the basal and one from the upper bone bed). They are cylindrical, laterally flattened, giving them an ovoid shape in occlusal view. The top of these teeth is covered by an ovoid translucent cap. Bunches of dentine tubules can be seen in occlusal view, but they lie underneath the translucent cap whose top is flat. The specimens have no preserved root.

Only one incisiform tooth was found, from the basal bone bed. The specimen is incomplete, lacking a great part of the root and the right posterolateral extremity. The tooth crown is eroded, the cutting edge being blunt. The narrower centre that usually slightly divides the crown into two lateral parts is still visible in occlusal view despite the abrasion.
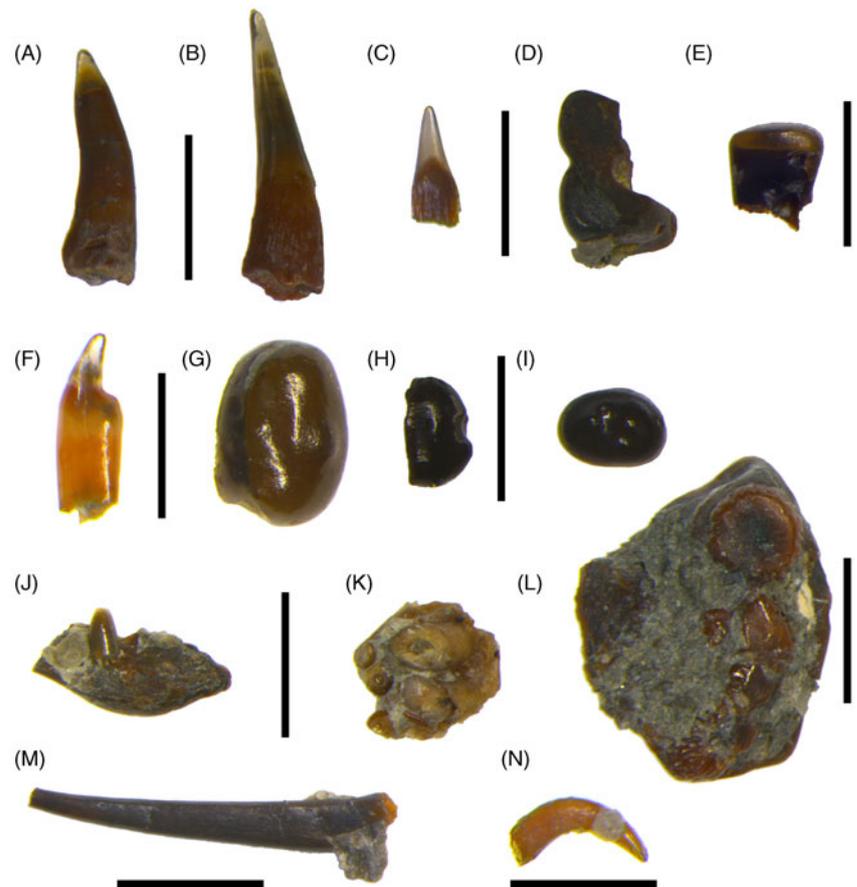
Figure 6. (Colour online) Osteichthyan teeth from the upper and basal bone beds at Blue Anchor Point. (A) *Gyrolepis* tooth BRSUG 29974-67 in lateral view. (B) *Birgeria* tooth BRSUG 29974-68 in lateral view. (C) *Saurichthys* tooth BRSUG 29974-176 in lateral view. (D, E) *Sargodon* teeth: (D) incisiform tooth BRSUG 29974-151 in occlusal view; (E) molariform tooth BRSUG 29974-63 in lateral view. (F) *Lepidotes* pharyngeal tooth BRSUG 29974-208 in lateral view. (G) *Lepidotes* tooth BRSUG 29974-141 in occlusal view. (H, I) *?Eomesodon* tooth BRSUG 29974-64 in lateral (H) an occlusal (I) views. (J) Jaw fragment with tooth BRSUG 29974-106 in lateral view. (K) Jaw fragment with teeth BRSUG 29974-100 in occlusal view. (L) Jaw fragment with teeth BRSUG 29974-105 in occlusal view. (M) Gill raker BRSUG 29974-74 in lateral view. (N) Pharyngeal tooth BRSUG 29974-191 in lateral view. Scale bar: 1 mm, except F and N: 500 μm.

4.b.5. Lepidotes sp. (Agassiz, 1832)

Twelve pharyngeal teeth (Figure 6F) were found in the basal bone bed, and they generally have broken tips. These teeth are cylindrical and flattened laterally, with a bulbous apex on the top of which a conical, translucent cap is laterally attached, sometimes giving to the tooth apex a hooked shape in lateral view.

These pharyngeal teeth were doubtfully allocated to *Sargodon tomicus* by Duffin and Gazdzicki (1977). However, more recent studies (Korneisel *et al.* 2015; Cavicchini *et al.* 2018) suggest that they belong to *Lepidotes*, based on their resemblance to branchial toothplates of *Lepidotes gloriae* Thies, 1989 (see Thies 1989, figure 10) from the Late Jurassic of Cuba.

Fifty-nine teeth, each with a cylindrical shaft and an apical translucent cap with a dome shape were also found and are tentatively attributed to *Lepidotes* (Figure 6G). Three of them are from the upper bone bed. This is also the case for 30 isolated caps that have been found in the basal bone bed, 27 of which have a reversed-bowl shape, with three of them having a more-or-less central tubercle on top of the cap. These caps are eroded, making it impossible to be sure whether the tubercle is in a central position or not, and whether the smoothness of the caps is the result of abrasion. Therefore, these three teeth could also belong to *Colobodus* (Sykes 1979).

This taxon has been used for these types of dome-shaped isolated teeth that do not correspond to any other taxon from the Triassic and Jurassic (López-Arbarello 2012; Nordén *et al.* 2015; Cross *et al.* 2018). In agreement with these studies, we refer these different teeth to *Lepidotes* despite the uncertainty.

4.b.6. ?Eomesodon sp. (Woodward, 1918)

One unexpected and distinctive tooth was identified in the basal bone bed (Figure 6H, I). It is a dome-shaped crown, with a crown of three dot-like cusps surrounding a central depression on the occlusal face of the tooth.

If correctly identified, this represents an important new record. This tooth resembles *Eomesodon liassicus* (Egerton 1854), from the middle Hettangian (Delsate *et al.* 2002, figure 29a, b). However, Triassic specimens of this genus are only known from the Norian Zorzino fauna of Italy (Tintori 2003; Tintori & Lombardo 2017), and the Norian and Rhaetian of Austria (Poyato-Arizona & Martín-Abad 2013; Schultz & Piller 2013; Hornung *et al.* 2019), although the corresponding species, *Eomesodon hoeferi* (Gorjanović-Kramberger 1905), could even belong to a new genus according to Ebert (2020). Pycnodontiformes, the order to which *E. liassicus* belongs, have not been found before in the Triassic of the UK, and are only present in the previously mentioned regions and the Germanic basin during the Late Triassic (Delsate & Kriwet 2004).

4.b.7. Other Osteichthyan remains

4.b.7.a. Unassigned Osteichthyan teeth. Twenty-eight elongate, conical teeth with a sharp acrodin cap and a broken shaft were found in the basal bone bed. They are too abraded to determine whether they belong to *G. albertii*, *B. acuminata*, or *S. longidens*.

4.b.7.b. Unassigned teeth with jaw fragments. Four unassigned teeth with jaw fragments have been found. One is from the upper bone bed, and is very abraded, with no tooth really protruding from

the jaw fragment. One of the other specimens from the basal bone bed is a single small tooth with a jaw fragment (Figure 6J). The tooth has an acrodin cap with a flat top but does not present any particular feature to help identify it. The last two, from the basal bone bed, are protruding teeth that all have broken crowns, making a more precise identification uncertain (Figure 6K, L).

4.b.7.c. Gill rakers. Five gill rakers have been found in the basal bone bed. The biggest specimen is 2 mm long (Figure 6M). The specimens have a slender, elongate, slightly curved and laterally flattened shaft. They all have a broken apex, and thus no cap is present, contrary to better preserved specimens found at other localities (e.g. Landon *et al.* 2017, figure 6H, I).

This type of specimen was previously identified by Duffin (1998a, 1999) as a gill raker of *Pseudocetorhinus pickfordi*, interpreted as a filter-feeding shark. However, this interpretation was questioned by Shimada *et al.* (2015) and these gill rakers are now thought to belong to an unknown Osteichthyan fish (Landon *et al.* 2017).

4.b.7.d. Pharyngeal tooth. One tooth with a hook-like shape has been found in the basal bone bed (Figure 6N). It could be an Osteichthyan pharyngeal tooth.

4.b.7.e. Scales. A total of 334 scale fragments were found, of which 89 come from the upper bone bed. Unfortunately, they are too eroded to determine whether they are *Gyrolepis albertii* scales, although 203 of them have a ganoine layer with a similar ridge pattern (Figure 7A) (see also Cross *et al.* 2018, Figure 4a, b). Nine scale fragments show the rectangular concentric pattern found under the ganoin layer as in Landon *et al.* (2017, figure 6L) and Cross *et al.* (2018, figure 11c).

4.3. Other fish remains

4.c.1. Vertebrae
Four abraded vertebral centra were found in the basal bone bed, with a flattened ring shape. Some may be Osteichthyan vertebrae, although this assumption is uncertain due to the state of these specimens (Figure 7B).

4.c.2. Fin rays
Nine fin ray fragments were identified, five from the upper bone bed and four from the basal bone bed.

4.4. Invertebrate fossils

4.d.1. Echinoid plates
Three fragments (Figure 7C) from the basal bone bed resemble echinoid plates as previously identified by Mears *et al.* (2016, figure 17i, j) and Landon *et al.* (2017, figure 7F, G). The specimens have a flat tile shape, and one side has a few regularly spaced little domes.

4.d.2. Gastropod steinkern
One gastropod steinkern fragment (Figure 7D) was found in the upper bone bed. The specimen presents only half a spiral revolution.

4.d.3. Coprolite
One slender, elongate, cylindrical coprolite with small darker particles on the surface was found in the basal bone bed. The specimen is 1 mm long.
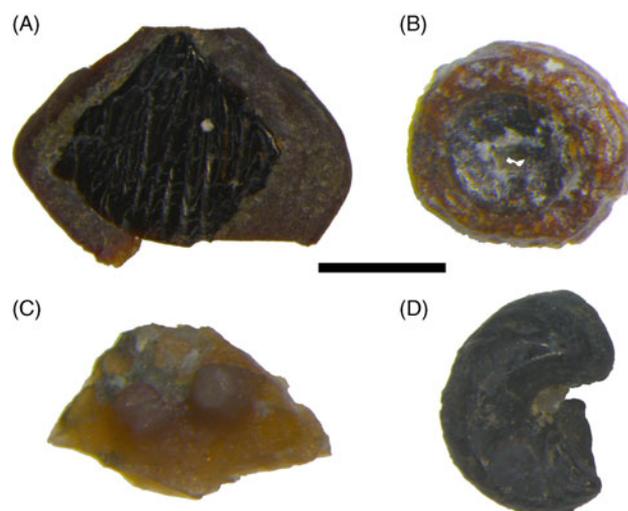

Figure 7. (Colour online) Other remains. (A) *Gyrolepis* scale BRSUG 29974-153 in exterior view. (B) Vertebra BRSUG 29974-73 in anterior or posterior view. (C) Echinoid plate BRSUG 29974-75. (D) Mollusc steinkern BRSUG 29974-50. Scale bar: 1 mm, except for B: 500 μm.

5. Discussion

5.a. Depositional environment

The presence of marcasite in the upper bone bed (Figure 3) and pyrite in both bone beds, alongside the occurrence of black shales and phosphatized remains throughout the deposits of Blue Anchor Point, indicate deposition under anoxic condition (Antia & Sykes 1979). The quite high level of abrasion of the specimens, such as scales that are all fragmentary, and the presence of sandy bone beds between the mudstones suggest that the bone beds include materials that have been removed from a location near the shore and transported offshore by storm events (Suan *et al.* 2012). This transportation during storm events is also supported by the presence of cream-coloured rip-up clasts in the basal bone bed that were torn off the Sully Beds underneath (Figure 2C), as at Doniford Bay (Tayler *et al.* 2023).

Like the other Rhaetian bone bed localities from the Bristol Channel area, Blue Anchor Point was located close to the Western Gate of the Central European Basin (Fischer *et al.* 2012; Whiteside *et al.* 2016). Also, like nearby Doniford Bay, St Audrie's Bay and Lilstock (Tayler *et al.* 2023; Lole Durbin *et al.* 2024), the site was probably several kilometres from shore when the bone beds were deposited. Deposition of bone bed materials in this distal site, probably in quite deep and thus anoxic and euxinic waters, preserved and phosphatized the vertebrate remains in the bone beds (Suan *et al.* 2012).

5.b. Faunal composition

Counts of 355 specimens from the upper bone bed and 647 from the basal bone bed were identified (Table 1). A third of the total number of specimens are scales. The fish teeth show clear differences between the two bone beds, with Osteichthyans dominant in the lower bone bed, chondrichthyans in the upper bone bed. In the basal bone bed, only 21 of the 135 counted specimens are chondrichthyan teeth (Figure 8A), *Lissodus* remaining the primary chondrichthyan taxon. *Lepidotes* is the most represented taxon, even without counting its gill rakers that are only present in the basal bone bed. *Gyrolepis*, *Lissodus* and

Table 1. Counts of taxa found in the basal and upper bone beds at Blue Anchor Point

	Basal bone bed		Upper bone bed	
	Identified	Counted	Identified	Counted
Chondrichthyan teeth				
Lissodus	20	16	66	38
Rhomphaiodon	12	4	41	24
Parascylloides	1	1	4	4
Synechodus	0	0	1	0
Pseudodalatias	0	0	1	0
?Pseudocetorhinus	4	4	0	0
Chondrichthyan indet.	6	0	124	0
Other chondrichthyan remains				
Morph 1 placoid denticles	45	45	3	3
Morph 2 placoid denticles	5	5	0	0
Morph 3 placoid denticles	1	1	0	0
Morph 4 placoid denticles	8	8	0	0
Placoid denticles indet.	2	0	0	0
Hybodontid denticles	2	2	1	1
Denticles indet.	3	0	0	0
Neoselachian vertebrae	0	0	2	2
Osteichthyan teeth				
Gyrolepis	64	33	2	1
Birgeria	16	15	4	3
Saurichthys	5	4	4	1
Sargodon	3	3	1	1
Lepidotes	89	59	3	1
Lepidotes gill rakers	12	12	0	0
?Eomesodon	1	1	0	0
jaw part with tooth	3	3	1	1
Gill rakers	5	5	0	0
Pharyngeal teeth	1	1	0	0
Osteichthyan indet.	82	0	1	0
Other osteichthyan remains				
Scales	245	245	89	89
Other fish remains				
Vertebrae	4	4	0	0
Bones	0	0	1	1

(*Continued*)

Table 1. (*Continued*)

	Basal bone bed		Upper bone bed	
	Identified	Counted	Identified	Counted
Fin rays	4	4	5	5
Other remains				
Echinoid plates	3	3	0	0
Gastropod steinkerns	0	0	1	1
Coprolites	1	1	0	0
Total	647	479	355	176

Birgeria represent most of the other taxa in the basal bone bed. Denticles are also mainly present in the basal bone bed. Indeterminate chondrichthyan teeth are the most represented teeth in the upper bone bed. Among the 73 counted specimens of the upper bone bed, the dominant taxon is *Lissodus*, followed by *Rhomphaiodon* (Figure 8B). The other taxa, including Osteichthyans, are far less represented.

The dominance of Osteichthyan taxa in the basal bone bed is unusual but matches what we observed at nearby Lilstock (Lole Durbin *et al.* 2024). However, there, the dominance by Osteichthyans applied to both the lower and upper bone beds. Further, the lower bone bed at the geographically closer locality of Doniford Bay is dominated by *Lissodus* teeth (Tayler *et al.* 2023). The dominance by Osteichthyans is seen also in the basal bone bed across the Bristol Channel at Lavernock, in South Wales (Evans *et al.* 2024). In all cases, including Blue Anchor, the locations are at the west end of the Rhaetian outcrop, closest to the western 'gate' from which the Rhaetian Transgression progressed, heading from southwest to northeast. Water flooded the Bristol–South Wales area from a gate to the emerging North Atlantic Ocean. These waters reached western localities such as Blue Anchor, Lilstock and Lavernock first and so faunas might be slightly older or might have occupied somewhat different habitats than those found further east.

What is even more surprising is the dominance of *Lepidotes* teeth at Blue Anchor. This is different from the English Rhaetian bone beds from other localities, where *Gyrolepis*, *Birgeria* and *Saurichthys* generally represent most of the Osteichthyan teeth (Cross *et al.* 2018) even when Osteichthyans are dominant (Allard *et al.* 2015; Mears *et al.* 2016; Cavicchini *et al.* 2018; Ronan *et al.* 2020; Williams *et al.* 2022; Lole Durbin *et al.* 2024). *Lepidotes* is only found in the basal bone bed of the Westbury Formation at Charton Bay, Devon, where there is a greater diversity of Osteichthyan taxa with no clear dominance (Korneisel *et al.* 2015).

The upper bone bed has a faunal composition similar to that of both bone beds at Doniford Bay (Tayler *et al.* 2023), and of the basal bone bed at Aust Cliff (Allard *et al.* 2015; Cross *et al.* 2018) and at sites along the M4–M5 motorway (Slater *et al.* 2016). This faunal composition with dominance of *Lissodus* and *Rhomphaiodon* over osteichthyan taxa represented by *Gyrolepis*, *Birgeria* and *Saurichthys* may be characteristic of offshore shallow marine environments (Tayler *et al.* 2023).

5.c. Differences between the two bone beds

Differences in faunal composition between the two bone beds could relate to differences in deposition. The upper bone bed is
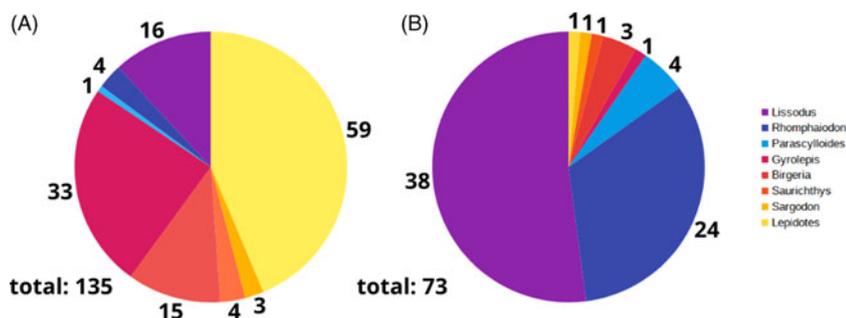
Figure 8. (Colour online) Pie chart presenting relative proportions of taxa counted from the basal (A) and upper (B) bone beds at Blue Anchor Point.

much richer in pyrite than the lower bone bed, and uniquely preserves marcasite, both suggesting more anoxic conditions. Both bone beds comprise detrital quartz grains and bone debris washed in from elsewhere, and the more anoxic conditions of the upper bone bed could indicate eventual deposition in deeper waters than the lower bone bed. Deposition of the upper bone bed in deeper water might reflect the generally rising sea level as the Rhaetian transgression proceeded.

5.d. Comparison of the Blue Anchor vertebrate fauna

Here, we review the key taxa from Blue Anchor, and their occurrences in the wider context of the Rhaetian bonebeds of England and across Europe.

Lissodus minimus was originally described (as *Acrodus minimus*) from the basal Rhaetian Bone Bed at Aust Cliff by Louis Agassiz (Agassiz 1839; Cross *et al.* 2018). Since then it has been recorded from virtually every Rhaetian site in the UK (e.g. Sykes *et al.* 1970; Allard *et al.* 2015; Korneisel *et al.* 2015; Nordén *et al.* 2015; Lakin *et al.* 2016; Mears *et al.* 2016; Slater *et al.* 2016; Landon *et al.* 2017; Cavicchini *et al.* 2018; Tayler *et al.* 2023; Lole Durbin *et al.* 2024) and throughout northwest Europe including France, Belgium, The Netherlands, Germany, Switzerland, Austria and Poland (e.g. Deecke 1926; Duffin & Gazdzicki 1977; Duffin 1980, 1985, 2001; Duffin *et al.* 1983; Duffin & Delsate 1993; Cuny 1995; Diependaal & Reumer 2021). Older German records suggest that the species is found in the Hauptmuschelkalk, Trochitenkalk, Keuperdolomit and Dachsteinkalk (Deecke 1926), giving a stratigraphic range of Ladinian to Rhaetian, although these records require verification.

Formerly *Hybodus minor*, *Rhomphaiodon minor* was also first described from the basal Bone Bed at Aust Cliff (Cross *et al.* 2018). Like *L. minimus*, it appears to be a standard member of the Rhaetian microvertebrate fauna, being found throughout the British Isles and northwest Europe, including the UK (e.g. Deecke 1926; Duffin & Gazdzicki 1977; Duffin *et al.* 1983; Duffin & Delsate 1993; Cuny 1995; Allard *et al.* 2015; Korneisel *et al.* 2015; Nordén *et al.* 2015; Lakin *et al.* 2016; Mears *et al.* 2016; Slater *et al.* 2016; Landon *et al.* 2017; Cavicchini *et al.* 2018; Diependaal & Reumer 2021; Williams *et al.* 2022; Tayler *et al.* 2023; Lole Durbin *et al.* 2024). Deecke (1926) also records it from the Lettenkohlesandstein (Middle Norian), and Struckmann (1871) records it from the Upper Muschelkalk (Ladinian) of Germany, records which require verification. Tackett *et al.* (2023) suggested that *Rhomphaiodon* sp. was part of a Late Triassic elasmofauna from Nevada (USA). Duffin (1993) described *R. minor* from the Steinmergelgruppe (Middle Norian) of Medernach in Luxembourg, giving it a suggested stratigraphic range from Ladinian to the Rhaetian.

Pseudodalatias barnstonensis was first described from the Rhaetian of Barnstone in Nottinghamshire (Sykes 1971) and,

although a rather rare component of Late Triassic faunas it has since been recorded from numerous Rhaetian sites in the UK (e.g. Sykes 1974; Allard *et al.* 2015; Nordén *et al.* 2015; Slater *et al.* 2016; Cross *et al.* 2018; Williams *et al.* 2022), France (Cuny 1995), the Netherlands (Diependaal & Reumer 2021), Belgium (Duffin & Delsate 1993) and Germany (Barth *et al.* 2014). Complete dental strips from the lower dentition have also been described from the Norian of northern Italy (Tintori 1980).

Synechodus rhaeticus (formerly assigned to *Palaeospinax*) was described from isolated dorsal fin spines from Rhaetian deposits at Aust Cliff and Holwell, and then on the basis of distinctive isolated teeth (Duffin 1982, 1998*b*) which have been recovered from numerous other sites in the UK (Allard *et al.* 2015; Nordén *et al.* 2015; Mears *et al.* 2016; Whiteside *et al.* 2016; Cavicchini *et al.* 2018; Ronan *et al.* 2020), Belgium and Luxembourg (Godefroit *et al.* 1998), Germany (Sander *et al.* 2016) and France (Cuny *et al.* 2000). *Pseudocetorhinus pickfordi* was also originally described from Holwell (Duffin 1998*a*). Its geographical range has since been expanded to include numerous other UK sites (Allard *et al.* 2015; Korneisel *et al.* 2015; Nordén *et al.* 2015; Mears *et al.* 2016; Slater *et al.* 2016; Cavicchini *et al.* 2018; Cross *et al.* 2018), plus outcrops in Germany (Barth *et al.* 2014; Sander *et al.* 2016), France (Cuny 1995; Cuny *et al.* 2000) and Luxembourg (Godefroit *et al.* 1998).

The tiny teeth of *Parascylloides turnerae* were probably long confused morphologically with posterior teeth of *Rhomphaiodon minor*. Since their original description from Barnstone in Nottinghamshire and the Hildesheim area of northern Germany (Thies *et al.* 2014) they have been recorded from a small number of Rhaetian sites in the UK (Cross *et al.* 2018; Moreau *et al.* 2021) and The Netherlands (de Lange *et al.* 2023).

The geographical and stratigraphical distribution of the various actinopterygian taxa found at Blue Anchor is quite similar to that of the chondrichthyan elements of the assemblage. Complete, articulated specimens of *Sargodon tomicus* occur in the Calcare di Zorzina (Middle Norian) and Argilliti di Riva di Solto (?Upper Norian) of the Italian Lombardy Alps (Tintori 1983), while isolated incisiform and molariform teeth have been recorded from the Rhaetian of Britain, France, Belgium, Germany, Switzerland, Austria and Poland (Deecke 1926; Duffin & Gazdzicki 1977; Duffin *et al.* 1983; Duffin & Delsate 1993; Cuny 1995; Sander *et al.* 2016). Tackett *et al.* (2023) note its presence in the Late Triassic fauna of Nevada while Deecke (1926) also records it from the Upper Muschelkalk (Ladinian) and Lettenkohle (Carnian) of Germany (cf. Deecke 1926), giving it a stratigraphic range of Ladinian to Rhaetian.

Birgeria acuminata and *Saurichthys longidens* were both established on material from the basal Rhaetian Bone Bed at Aust (Cross *et al.* 2018) and are common at Rhaetian localities throughout the UK (e.g. Sykes *et al.* 1970; Allard *et al.* 2015;

Korneisel *et al.* 2015; Nordén *et al.* 2015; Lakin *et al.* 2016; Mears *et al.* 2016; Slater *et al.* 2016; Landon *et al.* 2017; Cavicchini *et al.* 2018; Williams *et al.* 2022; Tayler *et al.* 2023; Lole Durbin *et al.* 2024). Both species have since been reported from Rhaetian deposits of France, Belgium, The Netherlands, Poland and Germany (Deecke 1926; Duffin & Gazdzicki 1977; Duffin *et al.* 1983; Cuny 1995; Barth *et al.* 2014; Sander *et al.* 2016; Diependaal & Reumer 2021). *Birgeria acuminata* ranges from the Upper Muschelkalk (Ladinian) to Rhaetian deposits according to Deecke (1926) and, outside the Rhaetian, *S. longidens* has also been reported from the Lettenkohle (Carnian). Tackett *et al.* (2023) report abundant remains of both taxa from the Late Triassic of Nevada.

Scales and teeth of *Gyrolepis albertii* have been recorded from Lower Muschelkalk (Anisian) to Rhaetian sediments (Deecke 1926; Duffin & Delsate 1993; Cuny 1995; Barth *et al.* 2014; Diependaal & Reumer 2021) throughout northwest Europe, as well as from the Late Triassic of Nevada (Tackett *et al.* 2023).

6. Conclusion

The Rhaetian at Blue Anchor Bay includes two bone beds in the Westbury Formation. These differ in their faunas, the lower bone bed containing abundant Osteichthyan teeth, and the upper bone bed being dominated by teeth of hybodont chondrichthyans. The lower bone bed is unusual when compared to those from other Rhaetian localities because normally the faunas of the basal bone bed are also dominated by chondrichthyan teeth. The absence of sharks at Blue Anchor is then a mystery. The upper bone bed, as elsewhere, contains more pyrite than the lower bone bed, as well as marcasite, both indicating more anoxic conditions and perhaps a deeper water deposition site.

Differentiation of the faunas could represent all sorts of biological and geological factors, but the dominance by Osteichthyans in the basal bone beds at western locations such as Blue Anchor, Lilstock and Lavernock, might indicate something about their geographic locations, closest to the source of the Rhaetian Transgression from the nascent Atlantic Ocean to the west. Perhaps, as the transgression flooded eastwards, there were sufficient differences in water depths or habitats, or even in the time it took, to be reflected in the faunal compositions.

References

Agassiz JLR (1832) Untersuchungen über die fossilen Fische der Lias-Formation. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde* **1832**, 139–49.

Agassiz JLR (1833–1843) *Recherches sur les poissons fossiles*. Tomes 1–3. Imprimerie Petitpierre, Neuchâtel. 390+34.

Allard H, Carpenter SC, Duffin CJ and Benton MJ (2015) Microvertebrates from the classic Rhaetian bone beds of Manor Farm Quarry, near Aust (Bristol, UK). *Proceedings of the Geologists' Association* **126**, 762–76.

Antia DDJ and Sykes JH (1979) The surface textures of quartz grains from a Rhaetian bone-bed, Blue Anchor Bay, Somerset. *Mercian Geologist* **7**, 205–10.

Barth G, Franz M, Heunish C, Kustatscher E, Thies D, Vespermann J and Wolfgramm M (2014) Late Triassic Norian-Rhaetian brackish to freshwater habitats at a fluvial-dominated delta plain (Seinstedt, Lower Saxony, Germany). *Palaeobiodiversity and Palaeoenvironments* **94**, 495–528.

Bonis NR, Ruhl M and Kürschner WM (2010) Milankovitch-scale palynological turnover across the Triassic–Jurassic transition at St. Audrie's Bay, SW UK. *Journal of the Geological Society* **167**, 877–88.

Boyd Dawkins W (1864) Outline of the Rhaetic Formation in West and Central Somerset. *Geological Magazine* **1**, 257–60.

Buckland W and Conybeare WD (1824) Observations on the south-western coal district of England. *Transactions of the Geological Society of London, Second Series* **1**, 210–316.

Cavicchini I, Heyworth HC, Duffin CJ, Hildebrandt C and Benton MJ (2018) A Rhaetian microvertebrate fauna from Stowey Quarry, Somerset, U.K. *Proceedings of the Geologists' Association* **129**, 144–58.

Cross SRR, Ivanovski N, Duffin CJ, Hildebrandt C, Parker A and Benton MJ (2018) Microvertebrates from the basal Rhaetian Bone Bed (latest Triassic) at Aust Cliff, S.W. England. *Proceedings of the Geologists' Association* **129**, 635–53.

Cuny G (1995) French vertebrates and the Triassic-Jurassic boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* **119**, 343–58.

Cuny G, Hunt A, Mazin JM and Rauscher R (2000) Teeth of enigmatic neoselachian sharks and an ornithischian dinosaur from the uppermost Triassic of Lons-le-Saunier (Jura, France). *Paläontologische Zeitschrift* **74**, 171–85.

Deecke, W (1926) Pisces Triadici. *Fossilium Catalogus* 33, 201 pp. Berlin.

De la Beche HT (1839) *Report on the geology of Cornwall, Devon and West Somerset.* Memoirs of the Geological Survey of Great Britain.

De Lange B, Chenal E, Diependaal HJ and Reumer JW (2023) Fish remains from the Rhaetian (Late Triassic) of Winterswijk, the Netherlands (Pisces: Chondrichthyes and Actinopterygii). *Netherlands Journal of Geosciences* **102**, e10.

Delsate D, Duffin CJ and Weis R (2002) A new microvertebrate fauna from the Middle Hettangian (Early Jurassic) of Fontenoille (Province of Luxembourg, south Belgium). *Memoirs of the Geological Survey of Belgium* **48**, 1–83.

Delsate D and Kriwet J (2004) Late Triassic pycnodont fish remains (Neopterygii, Pycnodontiformes) from the Germanic basin. *Eclogae Geologicae Helvetiae* **97**, 183–91.

Diependaal H and Reumer JWF (2021) Note on the Rhaetian fish fauna from a subrosion pipe in Winterswijk (the Netherlands), with a discussion on the validity of the genus *Severnichthys* Storrs, 1994. *Netherlands Journal of Geosciences* **100**, e9.

Duffin CJ (1980) The Upper Triassic section at Chilcompton, with notes on the Rhaetic of the Mendips in general. *Mercian Geologist* **7**, 251–68.

Duffin CJ (1982) A palaeospinacid shark from the Upper Triassic of south-west England. *Zoological Journal of the Linnean Society* **74**, 1–7.

Duffin CJ (1985) Revision of the hybodont selachian genus *Lissodus* Brough (1935). *Palaeontographica Abteilung A*, **188**, 105–52.

Duffin CJ (1993) Mesozoic Chondrichthyan faunas. 1. Middle Norian (Upper Triassic) of Luxembourg. *Palaeontographica A* **229**, 15–36.

Duffin CJ (1998a) New shark remains from the British Rhaetian (latest Triassic). 1. The earliest Basking shark. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1998**, 157–81.

Duffin CJ (1998b) New shark remains from the British Rhaetian (latest Triassic). 2. Hybodonts and palaeospinacids. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1998**, 240–56.

Duffin CJ (1999) Fish. In *Fossils of the Rhaetian Penarth Group. Field Guide to Fossils 9* (eds A Swif & DM Martill), pp. 191–222. London: Palaeontological Association.

Duffin CJ (2001) Synopsis of the selachian genus *Lissodus* Brough, 1935. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **221**, 145–218.

Duffin CJ (2009) "Records of warfare . . . embalmed in the everlasting hills": a history of early coprolite research. *Mercian Geologist* **17**, 101–111.

Duffin CJ, Coupatez P, LePage J-C and Wouters G (1983) Rhaetian (Upper Triassic) marine faunas from "Le Golfe du Luxembourg" in Belgium (Preliminary note). *Bulletin de la Société Belge de Géologie* **92**, 311–15.

Duffin CJ and Delsate D (1993) The age of the Upper Triassic vertebrate fauna from Attert (Province of Luxembourg, Belgium). *Professional Paper, Geological Survey of Belgium* **264**, 33–44.

Duffin CJ and Gazdzicki A (1977) Rhaetian fish remains from the Tatra Mountains. *Acta Geologica Polonica* **27**, 333–48.

Ebert M (2020) A new genus of Pycnodontidae (Actinopterygii) from the Upper Jurassic of France and Germany, included in a phylogeny of Pycnodontiformes. *Zoological Journal of the Linnean Society* **188**, 434–54.

Edwards RA (1999) *The Minehead district — a concise account of the geology: Memoir for 1:50 000 Geological Sheet 278 and part of sheet 294 (England and Wales).* British Geological Survey.

Egerton PMG (1854) On some new genera and species of fossil fishes. *Annals and Magazine of Natural History* **13**, 433–36.

Evans O, Duffin CJ, Hildebrandt C and Benton MJ (2024) Microvertebrates from the basal Rhaetian Bone Bed (Late Triassic) at Lavernock, South Wales. *Proceedings of the Geologists' Association* **135**, 321–344.

Fischer J, Voigt S, Franz M, Schneider JW, Joachimski MM, Tichomirowa M, Götze J and Furrer H (2012) Palaeoenvironments of the late Triassic Rhaetian Sea: implications from oxygen and strontium isotopes of hybodont shark teeth. *Palaeogeography, Palaeoclimatology, Palaeoecology* **353–355**, 60–72.

Foffa D, Whiteside DI, Viegas PA and Benton, MJ (2014) Vertebrates from the Late Triassic *Thecodontosaurus*-bearing rocks of Durdham Down, Clifton (Bristol, UK). *Proceedings of the Geologists' Association* **125**, 317–28.

Glen RA, Hancock PL and Whittaker A (2005) Basin inversion by distributed deformation: the southern margin of the Bristol Channel Basin, England. *Journal of Structural Geology* **27**, 2113–34.

Godefroit P, Cuny G, Delsate D and Roche M (1998) Late Triassic vertebrates from Syren (Luxembourg). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **210**, 305–43.

Gorjanović-Kramberger K (1905) Die obertriadische Fischfauna von Hallein in Salzburg. *Beiträge zur Palaeontologie und Geologie Oesterreich-Ungarns und des Orients* **18**, 193–224.

Gradstein FM, Ogg JG, Schmitz MD and Ogg GM (2020) *Geologic Time Scale 2020.* Amsterdam: Elsevier.

Hamilton D and Whittaker A (1977) Coastal exposures near Blue Anchor, Watchet and St. Audrie's Bay, North Somerset. In *Geological Excursions in the Bristol District* (ed RJG Savage), pp. 101–109. Bristol: University of Bristol.

Hauser LM and Martill DM (2013) Evidence for coelacanths in the Late Triassic (Rhaetian) of England. *Proceedings of the Geologists' Association* **124**, 982–87.

Hesselbo SP, Robinson SA and Surlyk F (2004) Sea-level change and facies development across potential Triassic–Jurassic boundary horizons, SW Britain. *Journal of the Geological Society* **161**, 365–79.

Horner L (1816) Sketch of the geology of the south-western part of Somersetshire. *Transactions of the Geological Society of London* **3**, 338–84.

Hornung T, Kogan I, Moosleitner G, Wolf G and Wielen J van der (2019) The Norian fish deposits of Wiestal ("Seefeld Member", Northern Calcareous Alps, Salzburg, Austria) – taxonomy and palaeoenvironmental implications. *Austrian Journal of Earth Sciences* **112**, 125–65.

Hounslow MW, Posen PE and Warrington G (2004) Magnetostratigraphy and biostratigraphy of the Upper Triassic and lowermost Jurassic succession, St. Audrie's Bay, UK. *Palaeogeography, Palaeoclimatology, Palaeoecology* **213**, 331–58.

Huene E. von (1935) Ein Rhynchocephale aus dem Rhät (*Pachystropheus* n. g.). *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* **74**, 441–47.

Korneisel D, Gallois RW, Duffin CJ and Benton MJ (2015) Latest Triassic marine sharks and bony fishes from a bone bed preserved in a burrow system, from Devon, UK. *Proceedings of the Geologists' Association* **126**, 130–42.

Korte C, Hesselbo SP, Jenkyns HC, Rickaby RE and Spötl C (2009) Palaeoenvironmental significance of carbon-and oxygen-isotope stratigraphy of marine Triassic–Jurassic boundary sections in SW Britain. *Journal of the Geological Society* **166**, 431–45.

Lakin R, Duffin CJ, Hildebrandt C and Benton MJ (2016) The Rhaetian vertebrates of Chipping Sodbury, South Gloucestershire, UK, a comparative study. *Proceedings of the Geologists' Association* **127**, 40–52.

Landon ENU, Duffin CJ, Hildebrandt C, Davies TG, Simms MJ and Benton MJ (2017) The first discovery of crinoids and cephalopod hooklets in the British Triassic. *Proceedings of the Geologists' Association* **128**, 360–73.

Lole Durbin O, Duffin CJ, Hildebrandt C and Benton MJ (2024) Microvertebrates from the basal Rhaetian Bone Bed at Lilstock, North Somerset. *Proceedings of the Geologists' Association* **135**, 181–95.

López-Arbarello A (2012) Phylogenetic interrelationships of ginglymodian fishes (Actinopterygii: Neopterygii). *PLoS One* **7**, e39370.

Lovegrove J, Newell AJ, Whiteside DI and Benton MJ (2021) Testing the relationship between marine transgression and evolving island palae-ogeography using 3D GIS: an example from the Late Triassic of SW England. *Journal of the Geological Society* **178**, jgs2020–158.

Mayall MJ (1981) The Late Triassic Blue Anchor Formation and the initial Rhaetian marine transgression in south-west Britain. *Geological Magazine* **118**, 377–84.

Mears EM, Rossi V, MacDonald E, Coleman G, Davies TG, Arias-Riesgo C, Hildebrandt C, Thiel H, Duffin CJ, Whiteside DI and Benton MJ (2016) The Rhaetian (Late Triassic) vertebrates of Hampstead Farm Quarry, Gloucestershire, UK. *Proceedings of the Geologists' Association* **127**, 478–505.

Moreau M, Duffin CJ, Hildebrandt C, Hutchinson D, Parker A, Carpenter S and Benton MJ (2021) Microvertebrates from the Rhaetian basal bone bed of Saltford, near Bath, SW England. *Proceedings of the Geologists' Association* **132**, 174–87.

Nordén KK, Duffin CJ and Benton MJ (2015) A marine vertebrate fauna from the Late Triassic of Somerset, and a review of British placodonts. *Proceedings of the Geologists' Association* **126**, 564–81.

Plieninger WHT von (1847) Zähne aus der oberen Grenzbreccie des Keupers bei Degerloch und Steinenbronn. *Jahresheft des Vereins für Vaterländische Naturkunde in Württemberg, Stuttgart* **3**, 164–67.

Poyato-Arizona FJ and Martín-Abad H (2013) History of two lineages: comparative analysis of the fossil record in Amiiformes and Pycnodontiformes (Osteichthyes, Actinopterygii). *Spanish Journal of Palaeontology* **28**, 79–90.

Quenstedt FA von (1858) *Der Jura. Part 5.* Tübingen: H. Laupp, 842 p.

Reif W-E (1978) Types of morphogenesis of the dermal skeleton in fossil sharks. *Paläontologische Zeitschrift* **52**, 110–28.

Richardson L (1911) The Rhaetic and contiguous deposits of west, mid, and part of eEast Somerset. *Quarterly Journal of the Geological Society of London* **67**, 1–74.

Ronan J, Duffin CJ, Hildebrandt C, Parker A, Hutchinson D, Copp C and Benton MJ (2020) Beginning of Mesozoic marine overstep of the Mendips: the Rhaetian and its fauna at Hapsford Bridge, Vallis Vale, Somerset, UK. *Proceedings of the Geologists' Association* **131**, 578–94.

Sander PM, Wintrich T, Schwermann AH and Kindlimann R (2016) Die paläontologische Grabung in der Rhät-Lias-Tongrube der Fa. Lücking bei Warburg-Bonenburg (Kr. Höxter) im Frühjahr 2015. *Geologie und Paläontologie in Westfalen* **88**, 11–37.

Schultz O and Piller W (2013) *Catalogus Fossilium Austriae. Band 3: Pisces.* Verlag der Österreichischen Akademie der Wissenschaften.

Shimada K, Popov EV, Siversson M, Welton BJ and Long DJ (2015) A new clade of putative plankton-feeding sharks from the Upper Cretaceous of Russia and the United States. *Journal of Vertebrate Paleontology* **35**, e981335.

Skinner M, Whiteside DI and Benton MJ (2020) Late Triassic island dwarfs? Terrestrial tetrapods of the Ruthin fissure (South Wales, UK) including a new genus of procolophonid. *Proceedings of the Geologists' Association* **131**, 535–61.

Slater TS, Duffin CJ, Hildebrandt C, Davies TG and Benton MJ (2016) Microvertebrates from multiple bone beds in the Rhaetian of the M4–M5 motorway junction, South Gloucestershire, U.K. *Proceedings of the Geologists' Association* **127**, 464–77.

Storrs GW (1993) Terrestrial components of the Rhaetian (uppermost Triassic) Westbury Formation of south-western Britain. *New Mexico Museum of Natural History and Science Bulletin* **3**, 447–51.

Storrs GW (1994) Fossil vertebrate faunas of the British Rhaetian (latest Triassic). *Zoological Journal of the Linnean Society* **112**, 217–59.

Storrs GW (1999) Tetrapods. In *Fossils of the Rhaetian Penarth Group. Field Guide to Fossils 9* (eds A Swift & DM Martill), pp. 223–238. London: Palaeontological Association.

Storrs GW and Gower DJ (1993) The earliest possible choristodere (Diapsida) and gaps in the fossil record of semi-aquatic reptiles. *Journal of the Geological Society* **150**, 1103–107.

Storrs GW, Gower DJ and Large NF (1996) The diapsid reptile *Pachystropheus rhaeticus*, a probable choristodere from the Rhaetian of Europe. *Palaeontology* **39**, 223–49.

Struckmann C (1871) Notiz über die Fisch- und Saurier-Reste aus dem oberen Muschelkalke von Warberg am Elm im Herzogthum Braunschweig. *Zeitschrift der Deutschen Geologischen Gesellschaft* **23**, 412–16.

Suan G, Föllmi KB, Adatte T, Bomou B, Spangenberg JE and Schootbrugge B van de (2012) Major environmental change and bonebed genesis prior to the Triassic–Jurassic mass extinction. *Journal of the Geological Society* **169**, 191–200.

Sykes JH (1971) A new dalatiid fish from the Rhaetic bone bed at Barnstone, Nottinghamshire. *Mercian Geologist* **4**, 13–22.

Sykes JH (1974) Teeth of *Dalatias barnstonensis* in the British Rhaetic. *Mercian Geologist* **5**, 39–48.

Sykes JH (1977) The Rhaetic bone-beds. *Mercian Geologist* **6**, 197–239.

Sykes JH (1979) *Lepidotes* sp.: Rhaetian fish teeth from Barnstone, Nottinghamshire. *Mercian Geologist* **7**, 85–91.

Sykes JH, Cargill JS and Fryer JG (1970) The stratigraphy, and palaeontology of the Rhaetic Beds (Rhaetian: Upper Triassic) of Barnstone, Nottinghamshire. *Mercian Geologist* **3**, 235–46.

Tackett LS, Zierer D and Clement AC (2023) Actinopterygian and chondrichthyan ichthyoliths reveal enhanced cosmopolitanism in Late Triassic marine ecosystems. *Historical Biology* **35**, 2022–35.

Tayler J, Duffin CJ, Hildebrandt C, Parker A and Benton MJ (2023) Geology and microvertebrate faunas of the Rhaetian Westbury Formation of Doniford Bay, Somerset. *Proceedings of the Geologists' Association* **134**, 166–82.

Thies D (1989) *Lepidotes gloriae*, sp. nov. (Actinopterygii: Semionotiformes) from the Late Jurassic of Cuba. *Journal of Vertebrate Paleontology* **9**, 18–40.

Thies D, Vespermann J and Solcher J (2014) Two new neoselachian sharks (Elasmobranchii, Neoselachii, Synechodontiformes) from the Rhaetian (Late Triassic) of Europe. *Palaeontographica, Abteilung A* **303**, 137–67.

Tintori A (1980) Teeth of the selachian genus *Pseudodalatias* Sykes, 1971 from the Norian (Upper Triassic) of Lombardy. *Rivista Italiana di Paleontologia i Stratigrafiya* **86**, 19–30.

Tintori A (1983) Hypsisomatic Semionotidae (Pisces, Actinopterygii) from the Upper Triassic of Lombardy (N. Italy). *Rivista Italiana di Paleontologia i Stratigrafiya* **88**, 417–42.

Tintori A (2003) The Norian (Late Triassic) Calcare di Zorzino Fauna from Lombardy (Northern Italy): the state of the art. *Rivista del Museo Civico di Scienze Naturali "Enrico Caffi" Bergamo* **22**, 53–7.

Tintori A and Lombardo C (2017) The Zorzino Limestone actinopterygian fauna from the Late Triassic (Norian) of the Southern Alps. In *The Late Triassic World* (ed LH Tanner), pp. 315–350. Amsterdam: Elsevier.

Warrington G, Audley-Charles MG, Elliott RE, Evans WB, Ivimey-Cook HC, Kent PE, Robinson PL, Shotton FW and Taylor FM (1980) A correlation of Triassic rocks in the British Isles. *Geological Society, London, Special Report* **13**, 1–78.

Warrington G, Cope JCW and Ivimey-Cook HC (1994) St Audrie's Bay, Somerset, England: a candidate Global Stratotype Section and Point for the base of the Jurassic System. *Geological Magazine* **131**, 191–200.

Warrington G and Whittaker A (1984) The Blue Anchor Formation (late Triassic) in Somerset. *Proceedings of the Ussher Society* **6**, 100–07.

Whiteside DI and Duffin CJ (2021) New haramiyidan and reptile fossils from a Rhaetian bedded sequence close to the famous 'Microlestes' Quarry of Holwell, UK. *Proceedings of the Geologists' Association* **132**, 34–49.

Whiteside DI, Duffin CJ, Gill PG, Marshall JEA and Benton MJ (2016) The Late Triassic and Early Jurassic fissure faunas from Bristol and South Wales: stratigraphy and setting. *Palaeontologia Polonica* **67**, 257–87.

Williams H, Duffin CJ, Hildebrandt C, Parker A, Hutchinson D and Benton MJ (2022) Microvertebrates from the Rhaetian bone beds at Westbury Garden Cliff, near Gloucester, UK. *Proceedings of the Geologists' Association* **133**, 119–36.

Woodward AS (1918) The fossil fishes of the English Wealden and Purbeck Formations, Part II. *Monograph of the Palaeontographical Society* **70**, 49–104.

Wright T (1860) On the zone of *Avicula contorta*, and the Lower Lias of the south of England. *Quarterly Journal of the Geological Society of London* **16**, 374–411.